

THE CONTEXT OF SONGS IN THE YELLOW WARBLER

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RECENT studies (Gill and Lanyon, 1964; Ficken and Ficken, 1965*b*) have shown that in some wood warblers (Parulidae) there are two distinct male songs, Accented Ending Song and Unaccented Ending Song. In some species Unaccented Ending Song appears to be primarily given to males of the same species, whereas Accented Ending Song is usually given to female mates and to males of other species. Although song in most passerines functions in the maintenance of territory and in the satisfactory completion of the breeding cycle, the possible interspecific function of song has not been widely recognized.

The purpose of this study was to investigate the two songs of the Yellow Warbler (*Dendroica petechia*) and to analyze their respective motivation and significance. The responses of this species and the closely related Chestnut-sided Warbler (*D. pensylvanica*) to each other were carefully noted.

Yellow Warblers were studied intensively during May–July, 1963–64, and June–July, 1965, thus encompassing the entire breeding cycle. Most investigations were conducted in two areas: Webster, Androscoggin Co., and Bremen and Damariscotta, Lincoln Co., Maine. Supplementary observations were made during May and June, 1964, in Tewksbury and Newburyport, Essex Co., Massachusetts.

Extensive field notes were made at the time of observations. Some of the birds were marked with regulation government bands plus small patches of Magic Marker applied to their feathers to facilitate identification of individuals.

The study areas in Maine (one in Webster, one in Damariscotta, and two in Bremen) are in each instance marshy areas invaded by an encroaching band of woody vegetation led by speckled alders (*Alnus rugosa*), willows (*Salix* sp.), and meadow sweet (*Spiraea latifolia*). Other prominent transitional species found outside this inner fringe of woody vegetation include red maple (*Acer rubrum*), and gray birch (*Betula populifera*). The study area at Webster is situated in an abandoned beaver pond; the other areas in Maine are old lakes that are gradually filling in with vegetation. The Tewksbury site is a marshy area partially covered with speckled alders and a few red maples. Studies made at Newburyport were in a sandy area fairly densely covered with bayberry (*Myrica pensylvanica*) and beach-plum (*Prunocerasus maritima*).

RELATION OF THE BIRDS TO THE AREA

In the northeastern United States the range of Yellow Warblers is particularly spotty and is the result of their fairly close adherence to wet areas not

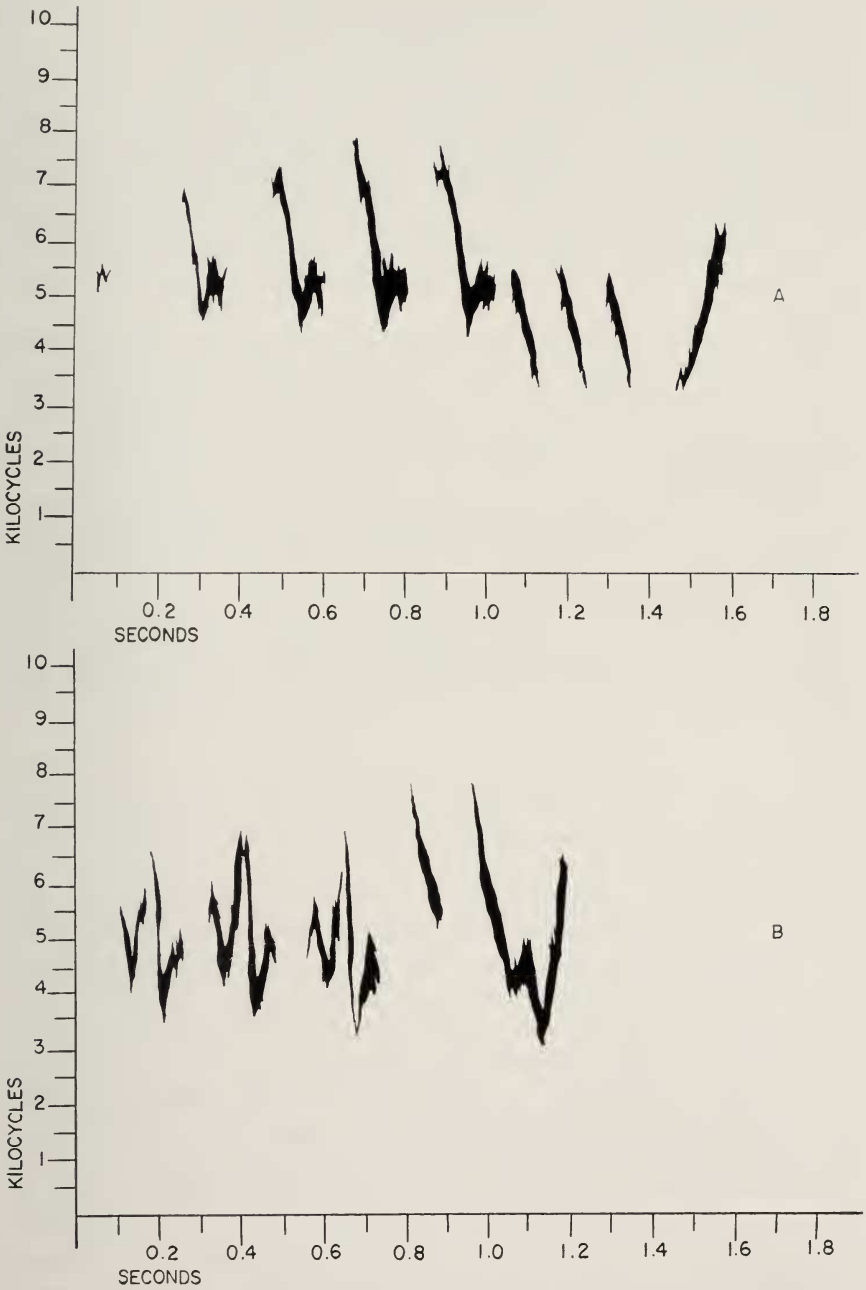


FIG. 1. Sound spectrograms of the vocalizations of Yellow Warbler: A, Accented Ending Song; B, Unaccented Ending Song.

completely covered by a tree canopy, to certain brushy areas, or to residential situations. The different species of warblers in and about relatively undisturbed wet areas are not separated ecologically in the same manner as the spruce-woods *Dendroica* warblers described by MacArthur (1958). Rather, their separation under natural conditions is a transitional one, as might be expected because of the steady habitat change often found in some of these areas. This change is particularly rapid about beaver ponds, the heightened water level being the result of dams built by beavers (*Castor canadensis*), which break soon after abandonment, and result in a secondary lowering of the water level.

Where available Yellow Warblers often used tall trees for singing perches, but also nested successfully in a few territories that did not contain elevated perches, apparently an important requirement of Yellow Warblers studied elsewhere by Kendeigh (1941) and Ficken and Ficken (1965a). The favored foraging and nesting habitat for Yellow Warblers in wet areas is on land partially covered by alders and willows from one and one-half to four meters tall, where they are usually the only *Dendroica* species found. The only other parulid regularly present is the Yellowthroat (*Geothlypis trichas*), which is a bird of the underbrush and apparently is not a close competitor. In the largest alders that are on the edge of the maple-birch zone and into that zone itself, Chestnut-sided Warblers predominate, in addition to American Redstarts (*Setophaga ruticilla*). Yellow Warblers are uncommon here.

RESULTS

The Yellow Warbler has two different songs, which are given in distinct situations (Fig. 1). Similar song types were recorded in this species by Ficken and Ficken (1965b).

Accented Ending Songs.—Accented Ending Songs were involved either with behavior performed about the female or about other species, notably Chestnut-sided Warblers (Table 1). This song predominated directly preceding and following copulation as well as about the nest while the female was incubating. If males had been singing an Unaccented Ending Song before coming in close contact with the female, they changed to Accented Ending Songs at that time. Accented Ending Songs were predominant prior to and during pair formation (Table 5). Many other times this song would also be given when from the context it was difficult to postulate why one pattern (or the other) would be chosen at that time. However, as the season progressed a strong tendency developed for Yellow Warblers to sing one particular song pattern in areas of previous experience of one sort or another. For instance, Accented Ending Songs would be delivered in the close vicinity of the nest even when the female was foraging a considerable distance away.

TABLE 1
APPARENT CONTEXT FOR SOME SONGS OF MALE YELLOW WARBLERS

Activity	Number of responses
<i>Loud Accented Ending Song</i>	
During and/or following presence of female Yellow Warbler	40
Copulation and/or female soliciting	9
Close proximity	11
Female fed on nest	11
Near nest occupied by female	8
Foreign female chased	1
During and/or following presence of male Chestnut-sided Warbler	
—singing on territory edge	23
Along Chestnut-sided Warbler territory edge in absence of Chestnut-sided Warbler	44
Prior to arrival of females in spring	heavily predominant (see Table 5)
<i>Loud Unaccented Ending Song</i>	
During and/or following presence of male Yellow Warbler on territory edge	68
Along Yellow Warbler territory edge in absence of other male Yellow Warbler	59
Intrusion of other Yellow Warbler into territory	22
Probable antiphonal singing between two males at greater distance than above	frequent
	N = 256

Where Yellow Warbler territories were bounded by Chestnut-sided Warbler territories, a strong tendency existed to give Accented Ending Songs along the edge bordering the Chestnut-sided Warbler territory in the male bird's presence and, especially after territories had been firmly established, even in its absence (see Table 2). Upon several occasions (including two interspecific fights) Yellow Warblers changed from Unaccented Ending Songs to Accented Ending Songs when they came into close contact with male Chestnut-sided Warblers, as might be expected if Accented Ending Song was being given in response to the male Chestnut-sided Warbler.

Unaccented Ending Songs.—Unaccented Ending Songs were heard at times that contact with other male Yellow Warblers was established (Table 1), almost every song preceding or following an actual overt hostile action being of this pattern (Table 3). In the few instances that normal volume Loud Accented Ending Songs were given immediately prior to overt hostilities, the singing birds probably were unaware of the individuals until the attack was launched. Unaccented Ending Songs also predominated when a male

TABLE 2
SONG PATTERN GIVEN ALONG EDGE OF OTHER WARBLER TERRITORIES BY YELLOW WARBLER

Pattern	Number of responses
<i>Chestnut-sided Warbler territory</i>	
Male Chestnut-sided Warbler absent	
Accented Ending Song	44
Unaccented Ending Song	9
Another male Yellow Warbler present	2
Another male Yellow Warbler singing on a boundary common to individual concerned	2
After fight with another male Yellow Warbler elsewhere	1
No explanation	2
Unaccented and Accented Ending Songs—no explanation	2
Male Chestnut-sided Warbler present	
Accented Ending Song (includes four fights)	23
Unaccented Ending Song—another male Yellow Warbler present and singing	5
<i>Yellow Warbler territory</i>	
Male Yellow Warbler absent	
Accented Ending Song—female Yellow Warbler nearby in evidence	2
Unaccented Ending Song	59
Male Yellow Warbler present	
Accented Ending Song	0
Unaccented Ending Song	68
	N = 210

sang along the border of a territory adjoining another Yellow Warbler territory in the male's presence and in its absence after territories had been firmly established (see Table 2). It was again difficult to determine at times why this particular song was sung, but a definite stereotypy with respect to past encounters was apparently an important factor in the production of this song in particular parts of the territory also. The strong tendency to sing Unaccented Ending Songs along the edges of other Yellow Warbler territories even in the absence of another male is an example of this phenomenon, and much of the data in Table 2 is the result of it. Responses were more predictable along borders shared with other Yellow Warblers than they were along borders shared with Chestnut-sided Warblers. Both along Yellow and Chestnut-sided warbler territory edges, the responses were slightly more predictable when both males were present than when one bird sang along a temporarily undefended edge. Other observations suggested that in addition to the development of stereotypy, unanalyzable song patterns in these birds were in large part the result of immediately preceding activities, the presence of other birds not seen by the observer, or both factors.

TABLE 3
SONG PATTERN IMMEDIATELY PRECEDING AND FOLLOWING OVERT HOSTILITIES
BETWEEN MALE YELLOW WARBLERS

Pattern preceding	Pattern following	Number of responses
Silent	Silent	1
Silent	Loud Unaccented	3
Muted Accented	Muted Accented	1 (one song, then Loud Unaccented)
Muted Unaccented	Silent	1
Muted Unaccented	Loud Unaccented	2
Loud Accented*	Silent	1
Loud Accented	Muted Unaccented	1
Loud Accented	Loud Unaccented	1
Loud Unaccented	Muted Accented	1
Loud Unaccented	Muted Unaccented	1
Loud Unaccented	Loud Unaccented	10
		—
		N = 23

* On the occasions that Loud Accented Ending Songs preceded overt hostilities, the birds involved appeared initially unaware of the other's presence, then attacked immediately.

Intermediate Songs.—Intermediate Songs were sometimes sung when the birds changed from one song pattern to another, and they appeared intermediate in motivation. This song type usually has a weak upslurred accented ending, but it is of an overall lackluster quality when compared to the Accented Ending Song. Intermediate Songs vary between typical Accented Ending Songs and typical Unaccented Ending Songs. Variations of Intermediate Song may be given by a single individual. The motivation resulting in production of Intermediate Songs may be comparable to that in Blackburnian Warblers (*Dendroica fusca*) (Morse, MS) and American Redstarts (Ficken, 1962) when they rapidly alternate their two basic song patterns. Neither of the two latter species appears to have a definite intermediate song. Yellow Warblers rarely if ever freely alternate Accented and Unaccented Ending Songs.

Silence and Muted Songs.—In moments of extreme aggression the birds were often silent, though occasionally Muted Unaccented Ending Songs were given (Table 4). Such phenomena were observed prior to or following a territorial encounter with another male, at a time that the two birds were situated very close to each other, or after a fight or chase. Ficken and Ficken (1965*b*) found similar responses in Yellow Warblers, Chestnut-sided Warblers, and American Redstarts. Occasional Muted Songs were also given during interactions between Yellow Warbler mates and between male Yellow Warblers and male Chestnut-sided Warblers. The occasional Muted Songs given in the

TABLE 4
ANALYSIS OF YELLOW WARBLER SONGS FOLLOWING SILENCE AND MUTED SONGS
RESULTING FROM INTRUSION OF OTHER INDIVIDUALS

Stimulus	Song at time of stimulus	Song following stimulus	Number of responses
Yellow Warbler, male	Silence	Silence	3
	Silence	Muted Accented	1
	Silence	Muted Unaccented	3
	Silence	Loud Unaccented	7
	Muted Accented	Silence	1
	Muted Accented	Muted Accented	1*
	Muted Unaccented	Loud Unaccented	4
Yellow Warbler, female	Silence	Muted Accented	1
	Silence	Loud Accented	2
	Muted Accented	Loud Accented	1
Chestnut-sided Warbler, male	Muted Accented	Loud Accented	3
			N = 27

* One song, then Loud Unaccented.

presence of female Yellow Warblers and male Chestnut-sided Warblers were always Accented Ending Songs.

Chestnut-sided Warbler songs.—Briefer work conducted on Chestnut-sided Warblers in the study areas indicated that the contexts of their songs, which can also be separated into Accented and Unaccented Ending Songs, are similar to those of the Yellow Warbler. Chestnut-sided Warblers usually sang Accented Ending Songs when in the immediate presence of female Chestnut-sided Warblers and along Yellow Warbler territory edges both in the presence of and absence of male Yellow Warblers. Accented Ending Songs preceded and followed four interspecific fights that I observed. At this time Muted Accented Ending Songs were given by some individuals of both species, but no Muted Unaccented Ending Songs were heard. Unaccented Ending Songs were also heard when males were in close contact with other male Chestnut-sided Warblers and when working along territory edges of other Chestnut-sided Warblers. The Accented Ending Songs of Chestnut-sided Warblers are extremely species specific, but their Unaccented Ending Songs closely resemble the Unaccented Ending Songs of Yellow Warblers.

Conditions of high density.—The Damariscotta marsh contained the largest number of Yellow Warblers of any study area, approximately eight in an area of two hectares. It was the only plot studied in which Yellow Warbler territories were considerably smaller than one-third hectare. Significantly, this area contained birds that produced many less Accented Ending Songs (Table 5), and the overt hostile behavior here was more frequent than in any other

TABLE 5

TIME SPENT SINGING ACCENTED AND UNACCENTED ENDING SONGS IN LARGE TERRITORIES
AND COMPRESSED TERRITORIES*

Date	Less than one-third hectare			One-third hectare or greater			Principal activity
	Acc.	Unacc.	Minutes	Acc.	Unacc.	Minutes	
Before 20 May	44.4	55.6	54	95.7	4.3	254	Before arrival of females and early arrival of females
20-31 May	13.6	86.4	44	47.2	52.8	671	Pair formation, nest building, egg laying
1-15 June	15.8	84.2	38	48.4	51.6	533	Incubation and early hatching
16-30 June	27.6	72.4	116	43.5	56.5	69	Young in nest and about nest
1-15 July	0.0	100.0	9	10.0	90.0	20	Young well fledged
			239			1547	

* Accented and Unaccented Ending Songs are recorded in percentages.

study area. Singing bouts and overt hostilities appeared to occupy the majority of the time and energy of the male birds through much of the breeding season. Fights and chases occurred more than five times as frequently here as they did in the Webster study area (1.7 fights and chases per hour to 0.3 fights and chases per hour), the difference in frequency being highly significant ($P < .001$). In Iowa, Kendeigh (1941) also noted a higher incidence of interactions where territories were very small than where they were larger. The individuals located in the areas of greatest density seldom if ever uttered Accented Ending Songs. Marginal individuals displayed a stronger tendency to produce Accented Ending Songs than did the central ones, especially on the part of their territory distal to the region of maximum concentration. In isolated pairs of Yellow Warblers there appeared to be the greatest tendency of all for the males to utter Accented Ending Songs, where moderate densities of the species occurred this tendency was lower, and where high densities occurred the tendency was lowest. Nevertheless, Unaccented Ending Songs were a conspicuous part of the repertoire of both the former groups of these birds. Unfortunately, my numerical data for lone birds are not sufficient for analysis.

Priority of activities.—Intraspecific territorial defense apparently claims priority over the activities usually associated with the Accented Ending Song, as suggested by observations of the birds of the Damariscotta marsh. When singing along Chestnut-sided Warbler boundaries, Yellow Warblers typically gave Accented Ending Songs, and Table 2 indicates that in 10 (and probably more) of the 14 exceptions when Unaccented Ending Songs were sung, another male Yellow Warbler was nearby. Similarly when a second male Yellow Warbler approached a pair during female solicitation or copula-

tion, the territorial male almost immediately gave chase, and changed to Muted Unaccented Ending Songs and then Loud Unaccented Ending Songs following the chase.

Seasonal change in song pattern.—Similar to Ficken and Ficken (1965*b*), I noted a seasonal change in song patterns (Table 5), which appeared correlated with various stages of the reproductive cycle. Although this change also occurred in the Damariscotta marsh, during the period that young were fledged there was a very significantly higher percentage of Unaccented Ending Songs under these conditions of high density ($P < .001$ through 15 June, $P < .05$ from 16 to 30 June, and probably not significant in a small number of observations after 30 June) than in other situations. Though Accented Ending Songs were curtailed in the birds located in the center of the Damariscotta study area, this pattern was most frequent about the edge of the marsh at the time of and prior to pair formation. Both central and peripheral birds all appeared to have obtained females, and there was no indication that the central birds experienced more than the usual difficulties in doing so. However, I have no data on the nesting success of these center birds compared to those on the periphery and individuals studied in other plots.

DISCUSSION

The contexts in which the two main Yellow Warbler songs are sung suggest the following motivations: Unaccented Ending Songs are given when there is a strong attack tendency or a conflict of the attack and escape tendencies. Accented Ending Songs on the other hand occur in situations in which these tendencies are not strongly activated.

The presence of species-distinct Accented Ending Songs in pairing and subsequent reproductive activities probably decreases the possibility of actual or attempted mixed pair formation in Yellow and Chestnut-sided warblers that might follow if Unaccented Ending Songs were used for this purpose. Though the plumages of these two species are distinctly different, their favored habitats are often so dense that song may be a particularly important initial factor in species discrimination, and a distinctive song may eliminate considerable confusion among them. Songs of a species-distinct type delivered in the presence of males of the opposite species allow territorial birds to distinguish between species. Yellow and Chestnut-sided warblers in the study areas only overlapped each other in habitat preference rather than using the same habitat. The information that a bird is of the opposite species may indicate that it does not constitute as important a challenge as a bird of the territory owner's species. On one of the few occasions that a Yellow Warbler was observed singing Unaccented Ending Songs on the edge of a Chestnut-sided Warbler territory when not in the presence of other male Yellow Warblers, a Chestnut-

sided Warbler was singing Unaccented Ending Songs nearby. Unaccented Ending Songs probably serve as a stronger threat of possible hostilities, both intraspecifically and interspecifically, than do Accented Ending Songs. The very indistinctness of the Unaccented Ending Songs of both species suggests an interspecific advantage (see Marler, 1957). This advantage may be that when a male bird strays into the other species' territory, any Unaccented Ending Songs given by the owner of the territory in the course of its activities serve to repress this intruder just as they would discourage a male of the same species as the territory holder.

Ficken and Ficken (1965*b*) noted that a Chestnut-sided Warbler singing only Unaccented Ending Songs was unsuccessful in obtaining a mate and that an American Redstart that sang only Unaccented Ending Songs was the last to obtain a mate. These observations suggest that at least in these two species, individuals using an Accented Ending Song at this time are more successful in obtaining a mate than are birds giving only Unaccented Ending Songs, but that at least in the American Redstart it is possible for a male to obtain a mate even if it lacks an Accented Ending Song.

Yellow Warblers in the Damariscotta marsh that sang very few if any Accented Ending Songs were successful in obtaining females and in maintaining the relationship through the breeding season. Males usually remained on the territories, which appeared well defined in contrast to the dense population of this species studied in a prairie community by Kendeigh (1941).

Yellow Warbler habitats, particularly those in the Damariscotta marsh, were often more open than those of the Chestnut-sided Warbler and American Redstart, and visual displays may form a more important part of pair formation than in the other two species. Also, the birds in the Damariscotta marsh probably were dominant individuals occupying optimal habitat rather than peripheral non-dominant birds. These individuals did not permit intrusions into their territories by other males to go unchallenged, as did the Chestnut-sided Warbler and American Redstart described by the Fickens. Perhaps the quality of the territory is of considerable importance in this species (see Ficken and Ficken, MS). Chestnut-sided Warblers and other closely related species were not observed in the middle of this marsh, so the use of the Accented Ending Songs in advertising to the female might not be as important here as in other areas where interspecific encounters occurred more often.

Though the Accented Ending Song is the pattern associated with the epigamic aspects of the breeding cycle it appears that it is of geologically younger origin than the Unaccented Ending Song, a conclusion also reached by Ficken and Ficken (1962) for several species of warblers possessing one essentially common song pattern. In 1961 and 1964 I studied three tropical members of this highly polytypic species, two of the "Mangrove" type (*D. p. bryanti* in

northwestern Yucatan and in British Honduras and *D. p. xanthotera* in southwestern Costa Rica) and one of the "Golden" type (*D. p. rufivertex* on Cozumel Is.) and found that all of these birds sang one pattern, comparable to the Unaccented Ending Song and subject to considerable variability. Bond (in Griscom and Sprunt, 1957) implies a similar situation in other West Indian "Golden" Warblers, stating that their songs resemble the nondescript ones of North American forms, though occasionally being more melodious. None of the forms that I studied frequent areas occupied by closely related species. West Indian forms are only found outside the isolated mangrove habitat on small islands, which have a depauperate fauna (see Bond, 1930).

Thus populations of this group lacking closely related sympatric species possess a single (though variable) song, while others with closely related sympatric species possess two distinct, though less variable, patterns. It appears probable in this case that the species-specific Accented Ending Song developed in response to interspecific pressure as a way of rapidly distinguishing Yellow Warblers from other closely related species.

The taxonomic treatment of the *Dendroica petechia* group has long been a matter of controversy (e.g., Peters, 1927; Aldrich, 1942; Griscom and Sprunt, 1957). The apparent ability of some North American Yellow Warblers to obtain mates without singing Accented Ending Songs suggests that song itself would not be a completely effective isolating mechanism between these individuals and the tropical ones, should the breeding ranges of the populations ever come together. Thus the absence of the species-distinct song in this case could not be considered an adequate reason in itself for splitting these forms.

SUMMARY

From 1962 to 1965 the songs and accompanying behavior of Yellow Warblers (*Dendroica petechia*) were studied in Maine and Massachusetts. Breeding Yellow Warblers frequent low alders and willows, where they often are the only nesting species of *Dendroica*. In more mature growth this species is largely replaced by the Chestnut-sided Warbler (*D. pensylvanica*). Yellow Warblers possess both Accented and Unaccented Ending Songs. Accented Ending Songs were almost always given in the presence of female Yellow Warblers or male Chestnut-sided Warblers. Unaccented Ending Songs were given in the presence of other male Yellow Warblers. As the season progressed these songs became associated with certain parts of a territory, even in absence of an obvious stimulus. Intermediate Songs were sometimes sung when birds changed song patterns and appeared intermediate in motivation to the two major patterns. Silence or Muted Songs often occurred when two male Yellow Warblers were in close contact, and also when in close contact with female Yellow Warblers or male Chestnut-sided Warblers. A very low incidence of Accented Ending Songs occurred in one study area where territories were small and competition intense, but these birds obtained mates. Unaccented Ending Songs are probably sung when a strong attack tendency or a conflict of attack and escape tendencies exist. Accented Ending Songs probably occur when these tendencies are not strongly activated. The existence of two different songs probably serves effectively in

species recognition where closely related sympatric species are present. Tropical populations of Yellow Warblers studied sang only Unaccented Ending Songs and were the only warblers in the habitat.

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